NEW YORK ENTOMOLOGICAL SOCIETY
92(2), 1984, pp. 162–168

FORAGING BEHAVIOR OF THE BEES *HALICTUS LIGATUS* (HYMENOPTERA: HALICTIDAE) AND *CERATINA CALCARATA* (HYMENOPTERA: ANTHOPHORIDAE): FORAGING SPEED ON EARLY-SUMMER COMPOSITE FLOWERS

Howard S. Ginsberg

Department of Ecology and Evolution, State University of New York,
Stony Brook, New York 11794

Abstract.—Pollen foraging *Halictus ligatus* and both pollen and nectar foraging *Ceratina calcarata* were timed on early-summer flowers on Long Island in New York State. Pollen-collecting *H. ligatus* worked inflorescences of *Erigeron annuus* (Asteraceae) more rapidly (ave. time 9.7 sec) than did *C. calcarata* (ave. time 18.3 sec). Handling time by nectar foragers did not differ significantly from pollen collectors of *C. calcarata.* Handling time was longer on young inflorescences of *E. annuus* that had numerous florets presenting pollen than on older inflorescences with fewer florets. *Halictus ligatus* worked inflorescences of *E. annuus* faster than the larger inflorescences of *Chrysanthemum leucanthemum* (Asteraceae). In addition to working inflorescences faster, *H. ligatus* flew between inflorescences faster than did *C. calcarata.* This suggests that handling time reflects the general pace of bee movement, which differs among bee taxa.

The amount of time bees take to forage on flowers is currently of considerable interest to students of pollination ecology. Indeed, handling time is an important component of contemporary theoretical approaches to foraging (Schoener, 1971; Pyke et al., 1977). However, the actual determinants of handling time on flowers are not yet well understood.

Several factors that influence foraging speed have been identified. There is evidence, for example, that bees that specialize on a flower species can work that flower more rapidly than can generalists, as has been shown for *Hoplitis anthocopoides* (Megachilidae) foraging for pollen on its host plant, *Echium vulgare* (Boraginaceae) (Strickler, 1979). Even among generalized foragers, handling times vary considerably among bee species on a given flower species. This undoubtedly results, in large part, from morphological characteristics of the bees and flowers.

Some authors have suggested that nectar foraging speed is directly related to tongue-length, bees with longer tongues being faster foragers (Brian, 1954; Holm, 1966; Benedek, 1973; Inouye, 1980). Others have proposed that the fastest foragers are those whose tongue-length best matches the corolla-length of the flower (Heinrich, 1976; Ranta and Lundberg, 1980). As might be expected, there is a great deal of variability in the relationship between tongue-length and foraging speed and there are several complicating factors. One is the influence of learning on foraging speed. Individual bumble bees, for example, forage more "accurately" (Heinrich, 1979) and thus more rapidly (Laverty, 1980) as they gain experience working a flower species. Another is that bees take longer working flowers with large amounts of nectar than flowers with little nectar (Thomson and Plowright, 1980; Hodges and Wolf, 1981).

Presumably, ambient temperature can also influence the pace of foraging (Linsley, 1958).

These complicating factors may explain some of the variability in the relationship between tongue-length and handling time (Ranta and Lundberg, 1980). However, it may also be that factors unrelated to tongue-length are major determinants of foraging speed. In the case of pollen-foraging bees especially, handling time may be quite independent of tongue-length. Among pollen foragers, simple correlations of foraging speed with morphological characteristics remain elusive. In the present study, I compare foraging times of two native, nonspecialist bee species on early-summer flowers in the northeastern United States, and examine some factors that may influence handling times on these flowers.

MATERIALS AND METHODS

I timed *Halictus ligatus* Say (Halictidae), a polyphagous, primitively eusocial, soil-nesting bee (Little, 1977; Michener and Bennett, 1977), on freshly-cut daisy (*Chrysanthemum leucanthemum,* Asteraceae) flowers in soda bottles with water. I set up 5 × 5 and 7 × 7 square arrays of regularly distributed flower stalks (50 cm between stalks) on a mowed field on the State University of New York campus at Stony Brook. *Halictus ligatus* can be easily distinguished from most other local bees, but because of their rapid movements in the field I may have mistakenly included a few moves by *H. rubicundus,* a similar species. Also, the process of cutting flowers and placing them in water undoubtedly influences nectar flow and may have modified handling times. The *H. ligatus* foragers were all pollen collectors but they often probed for nectar as well.

To avoid this problem for samples on fleabane (*Erigeron annuus,* Asteraceae), I found a dense patch of flowers and clipped unneeded flower stalks, leaving a 5 × 5 array (arranged as above) of intact flower stalks, presumably with undisturbed nectar and pollen flow. This array was located in a clearing in an open woodland in Nissequogue River State Park near Smithtown, Long Island, New York. I timed *H. ligatus* and *Ceratina calcarata* foraging on this flower array, and on 18 June 1981 I used a hand lens to count the number of florets presenting pollen in each inflorescence in the array.

Ceratina calcarata Robertson (Anthophoridae) is a polyphagous, solitary species that nests in plant twigs (e.g., sumac) that are hollowed-out by the females (Daly, 1973; Kislow, 1976). Female *C. calcarata* cannot be distinguished from *C. dupla,* another local species. However, males of these species are easily distinguishable and all males collected at the study site (N = 15) were *C. calcarata.* Thus, the females I studied were probably also *C. calcarata.*

I sampled *C. leucanthemum* from 26 May to 8 June, and *E. annuus* from 13 to 26 June, 1981. I recorded times on and between flower heads to the nearest one-tenth second with a Cronus digital sports timer. Air temperatures were recorded with a Springfield outdoor thermometer, hung in the shade approximately 0.5 m above the ground near the sample site.

I collected individuals of both bee species and placed them in Dietrich's solution for tongue-length measurements. I measured the labium of each bee under a stereo microscope with an ocular scale. I also measured lengths of corolla tubes of florets from heads of *E. annuus* at Nissequogue River State Park in 1982. Voucher specimens of the bee species were placed in the Cornell University Insect Collection, lot number 1114.

RESULTS

Disc florets of both flower species open in concentric circles around the center of the inflorescence, the outermost florets opening first. Bees that are small relative to the circle of florets follow the circle around the disc collecting nectar and/or pollen. Relatively larger bees stand in the center of the disc and rotate around the central axis, collecting resources from each floret. In general, bees make one revolution, but visits of greater and of less than one revolution are common.

The *Halictus ligatus* foragers (all pollen collectors) worked *Erigeron annuus* inflorescences more rapidly (mean = 9.7 sec, SD = 5.9, N = 57) than did pollen foraging *Ceratina calcarata* (mean = 18.3 sec, SD = 12.1, N = 37) (Wilcoxon 2-sample test, ts = 3.566, $P < 0.05$). In *C. calcarata* there was no significant difference (ts = 0.717) in handling time between pollen and nectar foragers (mean for nectar foragers = 20.8 sec, SD = 14.8, N = 77). It is relevant that pollen foragers generally probed florets for nectar as well. This probing may play a role in pollen collection. On intact stalks of *C. leucanthemum* in 1982, I observed *Ceratina* foragers probing florets with their proboscides, getting pollen dusted onto their heads and mouthparts, and then grooming this pollen onto their scopal hairs. The speed of pollen collecting may thus be related to the speed of nectar foraging in this genus.

The distance from the base of the prementum to the tip of the glossa is commonly used as an estimate of effective tongue-length in bees (Heinrich, 1976; Harder, unpubl. manu.). The prementum plus glossa of *C. calcarata* (mean length = 2.53 mm, SD = 0.177, N = 10) was slightly longer ($t = 7.12$, N = 20, $P < 0.01$) than that of *H. ligatus* (mean length = 2.04 mm, SD = 0.125, N = 10). These bees also differ in labial morphology; the glossa of *C. calcarata* is elongate, while that of *H. ligatus* (a "short-tongued" bee) is short and relatively obtuse. The average corolla-length of *E. annuus* was 1.90 mm (SD = 0.155, N = 50).

Handling time was not correlated with ambient temperature for either bee species (*H. ligatus*, $r = -0.015$, N = 57, $P > 0.9$; *C. calcarata*, $r = -0.152$, N = 155, $0.1 > P > 0.05$; Rohlf and Sokal, 1981:tables 12 and 25), although visits tended to be rapid at high temperatures (Fig. 1). Temperature is probably correlated with time of day and thus with resource levels in flowers, which may have influenced foraging speed. Handling time was more directly related to the number of open florets on a flower head (Table 1). Old inflorescences had fewer florets presenting pollen than did young inflorescences, and bees (*H. ligatus* at least) worked old flower heads faster than young ones. Also, florets in old inflorescences are clustered at the center of the disc while in young inflorescences they are scattered in a circle around the periphery of the disc, so bees have to cover more ground to work a young inflorescence.

Handling time by *H. ligatus* differed on different flower species. The average time on a daisy inflorescence was 12.7 sec (SD = 10.9, N = 25) while on fleabane it was 9.7 sec (SD = 5.9, N = 57; Wilcoxon 2-sample test, ts = 3.310, $P < 0.001$). This may reflect differences in inflorescence size, resource levels, or the number of open florets in each species, but note that the flower species were sampled at different times of

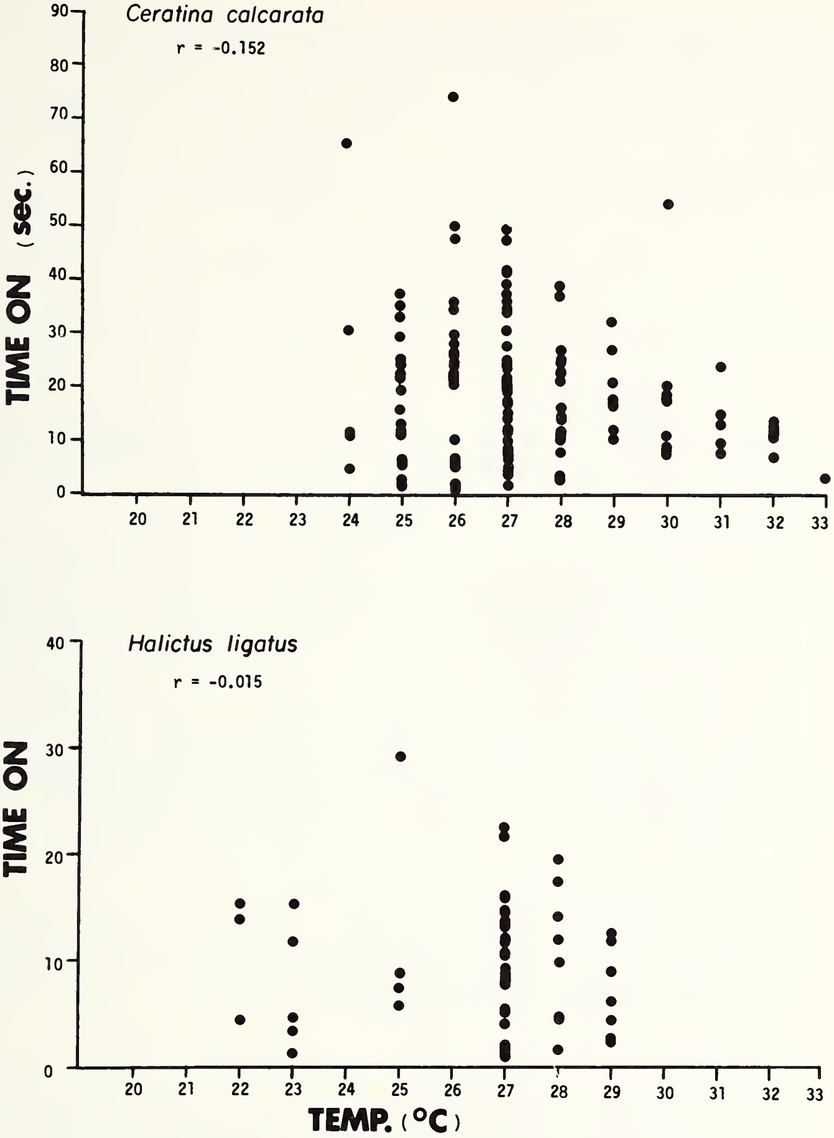

Fig. 1. Handling times on inflorescences of *Erigeron annuus* at different temperatures.

the season. Therefore, differences between overwintering gynes and later-generation workers may also have contributed to this difference in handling time.

Bees took longer to fly between inflorescences on different stalks than between inflorescences on the same stalk (Table 2). Also, in addition to working inflorescences

Table 1. Handling times of *Halictus ligatus* (Halictidae) and *Ceratina calcarata* (Anthophoridae) on *Erigeron annuus* (Asteraceae) as a function of age of inflorescence. (Time in seconds; sample sizes in parentheses. NS = not significant [Kruskal-Wallis tests].)

Age of inflorescence	*H. ligatus* ave. time on	*C. calcarata* ave. time on	Ave. # florets presenting pollen per inflorescence
Young	13.8 (13)	22.2 (37)	20.4 (61)
Intermediate	9.7 (10)	19.9 (31)	19.5 (51)
Old	3.9 (7)	12.7 (12)	8.7 (34)
Significance (alpha = 0.05)	*	NS	*

more slowly, *C. calcarata* flew between inflorescences more slowly than did *H. ligatus.* Thus handling time is correlated with the general pace of movement by the bee.

DISCUSSION

The fact that *Halictus ligatus* spent less time both on and between inflorescences than did *Ceratina calcarata* suggests that each species moves at a set pace that determines the speed of foraging on flowers. In nectar foragers, this pace may be partially set by the relationship between the tongue-length of the bee and the corolla-length of the flower (Ranta and Lundberg, 1980). However, the pace may also be set by any of a number of other factors, especially for pollen foragers. This general pace of foraging may, in fact, be a genus- or higher-level characteristic of bees. *Halictus* may move faster than *Ceratina* for physiological reasons unrelated to tongue-length. Intergeneric comparisons should therefore be made only with great care.

Halictus ligatus is larger than *C. calcarata* (Mitchell, 1960, 1962) and may thus be able to work an inflorescence more rapidly because it moves less between florets. Thus body size may be a correlate of foraging speed. Alternately, *H. ligatus* may simply work fewer florets per inflorescence than *C. calcarata.* My impression was that both species worked about the same number of florets on an inflorescence, but I have no quantitative data on this. Furthermore, this does not account for the difference in flight speed between inflorescences.

Table 2. Time spent flying between inflorescences of *Erigeron annuus* by *Halictus ligatus* and *Ceratina calcarata.* Time in seconds; standard deviation in parentheses. Significance of differences between flight times in each category by Wilcoxon 2-sample tests.

	Average time between inflorescences				
	On same stalk	N	On different stalks	N	
Halictus ligatus	0.6 (0.3)	35	1.3 (0.6)	19	$P < 0.001$
Ceratina calcarata	1.1 (0.9)	131	2.6 (1.3)	51	$P < 0.001$
	$P < 0.001$		$P < 0.001$		

The positive correlation of tongue-length with foraging speed found within the genus *Bombus* (Holm, 1966; Inouye, 1980) does not seem to apply in this case because the shorter-tongued bee in my study (*H. ligatus*) was the faster forager. *Halictus ligatus* does have a closer match of tongue-length to corolla-length of *E. annuus* than does *C. calcarata,* and this may explain its more rapid pace of foraging. However, both species collected pollen as well as nectar so tongue-length may be only marginally important. Nectar-collecting movements play a role in pollen collection by *Ceratina* on daisies, but this may not be true for other bees or on other flowers. Furthermore, my measure of tongue-length (length of prementum plus glossa) is not an accurate estimate of the effective tongue-length of these bees because they differ as to head width and labial structure. *Halictus ligatus* has elongate conjunctival thickenings basal to the prementum (Michener, 1944) that allow the mouthparts to swing forward, so its effective tongue-length may be longer than that of *C. calcarata* (which has only a short postmentum). Precise observations are needed on tongue-extension movements of these bees.

Handling time apparently does not vary with temperature, at least within the range I studied (Fig. 1), but it does differ on different flower species. It is not clear at this point to what extent the foraging pace on a given flower species varies within a bee species (in response to resource levels, etc.), and to what extent it is a fixed characteristic of that bee species. Studies of intra- and inter-taxon variability in bee foraging speeds on flowers with controlled amounts of nectar and pollen will help resolve this issue.

ACKNOWLEDGMENTS

I thank G. C. Eickwort, L. D. Ginsberg, J. D. Thomson, and an anonymous reviewer for constructive comments on early drafts of the manuscript. The staff members at Nissequogue River State Park were always helpful. This is contribution no. 472 in Ecology and Evolution at the State University of New York at Stony Brook.

LITERATURE CITED

Benedek, P. 1973. Relationship between the tripping rate and the tongue length of lucerne pollinating wild bees. Z. Angew. Ent. 73:113–116.

Brian, A. D. 1954. The foraging of bumble bees. Bee World 35:61–67, 81–91.

Daly, H. V. 1973. Bees of the genus *Ceratina* in America north of Mexico (Hymenoptera, Apoidea). Univ. Calif. Publ. Ent. 74:1–114.

Heinrich, B. 1976. Resource partitioning among some eusocial insects: bumblebees. Ecology 57:874–889.

Heinrich, B. 1979. "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. Ecology 60:245–255.

Hodges, C. M. and L. L. Wolf. 1981. Optimal foraging in bumblebees: why is nectar left behind in flowers? Behav. Ecol. Sociobiol. 9:41–44.

Holm, S. N. 1966. The utilization and management of bumble bees for red clover and alfalfa seed production. Ann. Rev. Ent. 11:155–182.

Inouye, D. W. 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumble bees. Oecologia 45:197–201.

Kislow, C. J. 1976. The comparative biology of two species of small carpenter bees, *Ceratina strenua* F. Smith and *C. calcarata* Robertson (Hymenoptera: Xylocopidae). Ph.D. thesis, Univ. Georgia, Athens, Ga.

Laverty, T. M. 1980. The flower-visiting behaviour of bumble bees: floral complexity and learning. Can. J. Zool. 58:1324–1335.

Linsley, E. G. 1958. The ecology of solitary bees. Hilgardia 27:543–599.

Litte, M. 1977. Aspects of the social biology of the bee *Halictus ligatus* in New York State. Insectes Sociaux 24:9–36.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Natur. Hist. 82:151–326.

Michener, C. D. and F. D. Bennet. 1977. Geographical variation in nesting biology and social organization of *Halictus ligatus*. Univ. Kansas Sci. Bull. 51:233–260.

Mitchell, T. B. 1960. Bees of the Eastern United States. Vol. 1. N. Carolina Agr. Exp. Sta. Tech. Bull. No. 141, 538 pp.

Mitchell, T. B. 1962. Bees of the Eastern United States. Vol. 2. N. Carolina Agr. Exp. Sta. Tech. Bull. No. 152, 557 pp.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52:137–154.

Ranta, E. and H. Lundberg. 1980. Resource partitioning in bumblebees: the significance of differences in proboscis length. Oikos 35:298–302.

Rohlf, F. J. and R. R. Sokal. 1981. Statistical Tables, 2nd edition. W. H. Freeman and Co., San Francisco, 219 pp.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

Strickler, K. 1979. Specialization and foraging efficiency of solitary bees. Ecology 60: 998–1009.

Thomson, J. D. and R. C. Plowright. 1980. Pollen carryover, nectar rewards, and pollinator behavior with special references to *Diervilla lonicera*. Oecologia 46:68–74.

Received April 19, 1983; accepted November 23, 1983.